



Primate Behavioral Ecology: From Ethnography to Ethology and Back

ABSTRACT Nonhuman primates occupy a special niche in anthropology because of the comparative insights into humans they provide. Initial anthropological interest in primates targeted the apes for their close phylogenetic relationships with humans, and the semiterrestrial Old World monkeys for their ecological similarities with hominids adapting to life on the ground. From the earliest anecdotal reports of tool use and hunting to more contemporary quantitative analyses of local "cultural" traditions, nonhuman primates have challenged deep-rooted concepts of human uniqueness and redefined the boundaries between us and other animals. Yet, despite the long-standing influence of primate studies in anthropology, approaches to studying primates began diverging from those of earlier ethnographers. Advances in primatology, particularly during the 1990s, have included a much deeper understanding of how ecology, phylogeny, and demography affect behavior. Insights into intraspecific, population-level variation represent an important area of convergence between primatology, other areas of anthropology, and conservation biology. [Keywords: primate behavioral ecology, anthropocentrism, evolutionary theory, systematic methods, biology]

PRIMATOLOGY IS A COMPARATIVE ENDEAVOR, especially in anthropology, in which nonhuman primates have always exerted a powerful influence on definitions of what it means to be human. Humans are more closely related to other primates than to other animals, and the African apes, particularly chimpanzees and bonobos, are the most closely related to us of all. Yet, despite our shared evolutionary history, deeply rooted cultural perceptions about nature–culture relationships have influenced the status of other primates, and of primatology, in anthropology.

Primates tend to be grouped categorically with other animals, in opposition to humans, in nature–culture dichotomies, and as intermediate, or "boundary species" between humans and other animals along nature–culture continua (Haraway 1989). Different academic traditions that have located primatology in either the social or biological sciences reflect underlying differences in whether primates are perceived as closer to humans or to other animals (Asquith 1991, 2000; de Waal 2001; Strum and Fedigan 2000). Independent of the ambiguous status of other primates, comparative insights into their natures continue to contribute to our understanding of human nature.

Primatology's development as a subfield within U.S. physical, or biological, anthropology dates back to the late 1950s, when Sherwood Washburn and his students began studying the behavior of wild primates for the insights

they could offer into human social evolution. U.S. physical anthropologists were not the first researchers to conduct field studies on wild primates, nor were the savannadwelling baboons initially targeted by Washburn and his student Irvan DeVore the only model for comparisons with humans. Even before DeVore began his dissertation research on olive baboons in Nairobi National Park, Kenya, Clarence Ray Carpenter (1934, 1940), influenced by psychologist Robert Yerkes, had already published monographs based on his field studies of mantled howler monkeys and gibbons. Influenced by Carpenter, Japanese primatologists had already cracked the code of matrilineal kinship in Japanese macaques (Kawai 1958; Kawamura 1958). In 1960, Jane Goodall began her long-term field study of the Gombe chimpanzees in Tanzania, stimulated by British paleontologist Louis Leakey's conviction about the comparative insights into hominids that the great apes would provide.

During its brief history as a discipline, primatology's relationship to other areas of anthropology has changed dramatically. This change has been largely, but not entirely, in response to what primates have revealed about themselves. As knowledge from an increasing diversity of primates began to accumulate, the emphasis in primatology began to shift from identifying the most appropriate "referential" models for comparisons with humans to identifying the underlying principles that could explain

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patterns of primate behavioral evolution more broadly (Tooby and DeVore 1987). By 1981, when Alison Richard's article "Changing Assumptions in Primate Ecology" appeared in the *American Anthropologist* (1981:517–533), the future of primatology in anthropology looked exceedingly grim. Primatologists, for the most part, had by then replaced the descriptive, ethnographic approaches of anthropology with the evolutionary framework and quantitative methods of ecology and biology. Primates became increasingly interesting in their own right, as intelligent, socially complex animals (Rowell 1993, 2000) that could be studied with the same methodologies employed by ethologists and behavioral ecologists.

As a result of these changes in perceptions and methods, primatology embarked on what seemed to be an irreversible trend that would lead to its inevitable realignment with biology. By the 1980s, it was not uncommon for nonbiological anthropologists to question what primatology could contribute to the rest of anthropology. Even now, primatologists seeking employment in anthropology departments are well advised to anticipate this question from prospective colleagues (Fedigan 2000). Yet, while the 1970s revelations about primate behavior patterns were strongly influenced by biological approaches that pulled primatology away from anthropology, those of the late 1990s, which emphasized intraspecific, population-wide variation, have begun to rekindle an interest among primatologists in anthropological approaches to explaining human cultural variation.

In this article, I pick up primatology's relationship to anthropology where Alison Richard (1981) left off. Specifically, I consider how the changing assumptions about primates that occurred in the 1970s affected the expansion of primatology in the 1980s, and how this expansion affected the development of comparative models of primate behavioral variation that pivot around ecology, phylogeny, and, more recently, demography. Together with theoretical and methodological transitions, the unit of analysis in primatology has shifted from individual informants representing their respective species to include populations and dynamic group processes over time. Contemporary primatology is now focused around the dual challenges of understanding the proximate mechanisms that underlie behavior and of reconciling deterministic, ecological, and phylogenetic models of behavior with fluctuating stochastic demographic processes. Opportunities for understanding intraspecific, population-level variation have grown as the number of long-term studies has increased. Comparisons among primate populations, like those among humans, may be uniquely influential in reinforcing primatology's place within anthropology.¹

I do not attempt a comprehensive review of either the history or major advances in primatology, both of which are beyond the scope of this article and discussed in other recent sources (e.g., Rodman 1999; Strier 2002a; Strum and Fedigan 2000; Sussman 2000). Instead, I focus on some of the most influential theoretical perspectives and

methodological approaches that have steered primatology's course from ethnography, to ethology, and back.²

ETHNOGRAPHIC ORIGINS

The early anthropologically oriented field studies focused on the comparative perspectives that the behavior of other primates could provide about humans. Underlying assumptions about the primary forces that shaped human social evolution dictated which species were targeted for study and which aspects of primate behavior were of greatest interest. Assumptions about the role of ecology stimulated field studies on savanna-dwelling baboons, while assumptions about the role of phylogeny provided the impetus for field studies on chimpanzees. At the time of these initial field studies, the mechanisms by which both ecology and phylogeny influenced behavior were only vaguely understood, but they nonetheless set the stage for the parallel, and yet mutually informative, paths that ecological and phylogenetic approaches in primatology have followed.

Washburn and DeVore's (1961) initial fieldwork with savanna-dwelling baboons was predicated on the assumption that baboons and our hominid ancestors found similar social solutions to meet the similar ecological conditions they faced. In those days, the decisive first step in early human evolution was thought to have occurred when the first hominids exchanged the relative safety of trees for a more terrestrial, and bipedal, way of life. Both the baboons and early hominids that populated the East African savannas would have encountered similar challenges of detecting and avoiding terrestrial predators, and of finding and defending dispersed resources such as food, water, and shelter, all of which necessitated social responses.³

The large, cohesive, multimale, multifemale, hierarchical groups of savanna-dwelling olive baboons differed markedly from those of the more relaxed Indian langur monkeys studied by Phyllis Dohlinow (previously, Jay 1968), another Washburn student, as well from the societies of forest-dwelling monkeys, including other populations of olive baboons (Rowell 1966) and other species of baboons (e.g., chacma baboons, Hall 1963). The behavioral differences between savanna baboons and the forest-dwelling monkeys known at the time were consistent with ideas about the effects of predators on the size and composition of primate groups (e.g., Crook and Gartlan 1966) and the evolution of primate societies (Goss-Custard et al. 1972). Male savanna baboons are larger than females in both body and canine size, which was presumed to reflect their roles as the leaders and protectors of their groups. The complex social relationships that seemed to preoccupy adult males as they vied, whether independently or with allies, for their positions in the hierarchy were seen as a consequence of the constant associations in large groups that life on the savanna required.

Leakey's interest in the behavior of the great apes, in contrast, was predicated on the idea that the best comparative models for hominids would be found among our

closest living hominoid relatives. The closer evolutionary relationship between humans and apes, as compared to that of humans and monkeys, was recognized long before paleoecological evidence indicated that woodlands might have been more likely habitats for early hominid evolution than savannas. It was also long before modern molecular genetics revealed a much more recent common ancestry, of just six to eight million years, between the ancestors of today's African apes and humans than was previously thought (Marks 2002).

The first anecdotal reports of tool use and hunting by chimpanzees (Goodall 1968) were particularly influential in reinforcing chimpanzee-based comparisons with humans. Both tool use and hunting were thought to be prime movers of human evolution and, therefore, traits that distinguished humans from other primates. Evidence of similar behavioral tendencies in chimpanzees implied that our last common ancestors might have had these tendencies as well.

The societies of apes also deviated from those of the increasingly familiar Old World monkeys in ways that were consistent with differences in their respective kinship systems. In contrast to most of the familiar Old World cercopithecines, such as baboons and macaques, none of the apes live in extended matrilineal societies. The fact that chimpanzees, like many extant human foragers, live in patrilineal societies was consistent with ideas about the importance of male cooperation for large game hunting during hominid evolution as well. The matrilineal societies of baboons and macaques came to be regarded as the "typical" primate social pattern from which both chimpanzees and hominids diverged. That this "myth of the typical primate" prevailed long after contradictory evidence from a greater diversity of primates had accumulated is a testimony to the resilience of anthropocentric ideas about the distinctiveness of humans, along with their closest phylogenetic relatives, compared to the rest of the primate order (Strier 1994a, 2001a; Sussman 2000).

ETHOLOGY AND EVOLUTIONARY BIOLOGY

In addition to dictating which species of primates were initially studied, the early ecological and phylogenetic approaches in primatology carried different sets of assumptions about the degree to which the basic components of sociality, such as grouping patterns or kinship systems, responded facultatively to external conditions or were phylogenetically constrained (Crook and Gartlan 1966; Gartlan 1973; Goss-Custard et al. 1972; Struhsaker 1969). Regardless of which underlying assumptions and corresponding approaches were favored, anthropological interest in primates still converged on the comparative insights into humans they could provide (Fedigan 1982).

The first wave of primate field studies, spanning from Carpenter's pioneering work in the 1930s through the various studies on Old World monkeys and apes launched in the 1960s, were accessible to other anthropologists be-

cause they resembled, for the most part, ethnographies. Primate fieldworkers produced rich, descriptive accounts of social behavior based on carefully annotated observations and detailed anecdotes. Primatologists were often participatory observers, provisioning their subjects with food to facilitate the habituation process and to create contexts that increased their opportunities to observe social interactions (Asquith 1989). Observations, for the most part, were based on recognizable individuals routinely referred to by name, and the boldest individuals in these study groups served as "informants" into the social customs and relationships on which their societies were based. Like ethnographers, the early primatologists were cognizant of the biases inherent in their methods, but the standards for systematic behavioral sampling and quantitative analyses that characterize contemporary primatology had not yet been established.

Shifting Methods and Theories

The widespread adoption of systematic, quantitative methods occurred in the 1970s, in large part because these methods, promoted by psychologists and biologists (e.g., Altmann 1974; Crook and Gartlan 1966; Hall 1962), reduced observer biases and therefore facilitated comparisons among studies.⁴ By sampling behaviors of interest at predetermined intervals, the relative frequencies or rates at which social interactions occurred could be compared across the same or different species and studied by the same or different researchers at different times. By sampling a wide range of individuals, the variation in behavioral patterns within and between study groups could be quantified and statistically compared. Thus, instead of subjective assessments by observers about whether one species, or one sex, is more aggressive than the other, quantitative analyses permitted more objective comparisons of the actual rates at which aggressive interactions occur (Sussman and Garber 2002).

Researchers' biases continued to influence what kinds of questions were asked and what kinds of behaviors were sampled, both of which have contributed to shifts in our perceptions of primates as aggressive and competitive to more conciliatory and cooperative (e.g., de Waal 2001; Haraway 1989; Silverberg and Gray 1992; Strum and Fedigan 2000). Presumably, however, any trained observer using similar definitions of aggressive or affiliative behaviors, and similar sampling protocols, would obtain results comparable to another's.

Quantitative analyses of systematic behavioral data were a powerful tool, not only for interspecific comparisons, such as those between baboons and chimpanzees, but also for intraspecific comparisons, such as those between savanna- and forest-dwelling baboons or among individuals, whether by sex, age, rank, or kinship, within single study groups. Previously qualitative descriptions of different social patterns in baboons and chimpanzees could be replaced with comparative data on the actual proportion

of their time individuals spent in proximity or interacting with one another. Similarly, anecdotal accounts of different mothering styles could be tested against predictions based on their correlation with maternal ranks, age, experience, or other attributes that distinguish one mother from another (e.g., Altmann 1980).

Systematic methods of behavioral sampling had also become necessary for evaluating the new evolutionary hypotheses about behavior that were being developed at the time. Advances in evolutionary theory provided ways of formulating questions about primate sociality in terms of the same kinds of selection pressures that lead to the evolution of other adaptive traits. As adaptations, primate social behaviors have evolved in response to local selection pressures acting on existing genetic variation in their populations. Variation in behavior, like variation in any other biological trait with a genetic basis, should, therefore, have consequences on individual fitness, as reflected by the variance in their genetic contributions to future generations.

Evolutionary theories about behavior and its consequences for the survival and reproductive success of individuals generated testable predictions, instead of ethnographic-type descriptions. Systematic sampling methods and quantitative analyses were the means by which predictions about behavioral adaptations could be evaluated. Together, evolutionary theory and quantitative methods for collecting and analyzing data were instrumental in transforming primatology into a hypothesis-driven science.⁵

Predictive Models

By the end of the 1970s, comparative studies of other animals, including birds, bats, and ungulates, were generating models about the relationships between ecological variables, like food and predator pressures, and social variables, such as grouping patterns and mating systems (Bradbury and Vehrencamp 1977; Emlen and Oring 1977; Jarman 1974). These ways of characterizing, measuring, and relating social behavior to ecological variables in other animals were applicable for primates as well, and formed the foundation for a new series of comparative socioecological models in primatology.

Among the fundamental features of these new models was the differential treatment of males and females based on differences in their reproductive biology that affected their reproductive potential. Briefly, evolutionary theory predicted that both sexes were selected to behave in ways that optimized their access to the resources most critical to their survival and reproductive success (Trivers 1972). Differences in the spatial distribution and temporal availability of food resources became the focus for interpreting variation in female social relationships and grouping patterns, while the spatial distribution and temporal availability of fertile females became the focus for interpreting variation in male social strategies. The variety of social systems primates exhibited was assumed to reflect compro-

mises between males and females responding to diverse conditions of food and mate availability (van Schaik 1983, 1989; Wrangham 1979, 1980).

Gaining access to critical resources involves social trade-offs, which vary with local ecological conditions. These trade-offs should be reflected in relative fitness costs and benefits, leading to evolutionary compromises in so-called optimal behaviors. Models of optimal group size, for example, predicted trade-offs between the costs and benefits of group living associated with increased competition for resources and increased predator detection and avoidance, respectively (Maynard Smith 1978). Similarly, models of sociality predicted trade-offs between competition and cooperation in acquiring and defending resources from other group members and other groups of conspecifics. Evolutionary theories of kin selection (Hamilton 1964) generated specific predictions about the conditions under which biological kin should be more inclined to cooperate with one another than with nonkin, while reciprocal altruism could explain the conditions under which nonkin might nonetheless behave altruistically toward one another (Trivers 1971). Evolutionary and ecological models thus provided a quantitative framework for explaining primate social evolution in ways that qualitative comparisons with humans could not.

Sexual selection, which dates back to Charles Darwin's 1871 classic, *The Descent of Man and Selection in Relation to Sex*, was also invoked to understand why males and females look and behave so differently from one another. Hypotheses about the trade-offs that males and females impose on one another while in pursuit of their own survival and reproductive success were predicated on the irrefutable sex differences in their respective reproductive biology.⁶

Feminism and Primatology

The adoption of evolutionary theories that emphasized the biological differences between males and females both coincided and conflicted with the expansion of feminist perspectives in other disciplines (Hrdy 1981, 1986; Tang-Martinez 2000). The development of feminist perspectives in primatology emphasized the influence of females on both males and their emergent societies and shifted some of the focus away from the sensational hair-raising displays of large, showy, and often explosive males toward the more subtle behavioral tactics that females employed in their day-to-day interactions with one another and with males. Studies focusing on female primates revealed them to be autonomous actors whose behaviors impacted their social environments, often in ways that correlate with enhanced reproductive success. Female primates could no longer be regarded as passive "resources" over which males competed, and interpretations of male behavior became increasingly dependent on the constraints and compromises imposed by females.

The increased attention paid to female primates significantly altered the perceptions of primate societies. These enlightened perceptions have often been attributed to the influx of feminist-oriented primatologists, particularly, but not exclusively, women who entered the field during the 1970s (e.g., Haraway 1989). However, it is also the case that evolutionary theories, including kin selection and sexual selection, being adopted at the time were similarly influential because of their emphasis on the importance of females and the effects of female behavior on that of males (Emlen and Oring 1977). Socioecological models, with their specific predictions about how the behavior of males should map onto that of females, which in turn should map onto the distribution and availability of food and other resources, converged with feminist perspectives in primatology to stimulate interest in the behavior of females and the powerful influence they can exert in their societies.

FROM ETHNOGRAPHY TO ETHOLOGY

Feminist perspectives might have helped to sustain the connections between primatology and other areas of anthropology, in which similar attention was being paid to females and their power in societies. Yet, by accepting the influence of sex differences in reproductive biology on the behavior of females and males, even the most thoughtful and articulate primatologists often found themselves at odds with feminist scholars from other disciplines in which biological sex differences were not acknowledged, and, therefore, the influence of biology on behavior was not admissible. Feminist approaches in primatology were rooted in the unifying principles of evolutionary biology, which led to predictions about sex differences in behavior. However much the empirical data confirmed the social empowerment of female primates, the premise that biology underlies sex differences was inconsistent with some of the other kinds of feminism being practiced by other scholars.

The more general search for unifying principles in primatology was itself antithetical to the expansion of cultural relativism and postmodernism in cultural anthropology. This was especially true coming, as it did, on the heels of E. O. Wilson's (1975) *Sociobiology: The New Synthesis* and the misunderstandings about biological determinism ([sic] genetics) versus biological potential ([sic] genotype—environment interactions) that sociobiology engendered. Anthropology was still reacting against social Darwinism and the eugenics movement, and evolutionary ideas about the genetic basis underlying the behavior of primates, which by definition included humans, received a critical reception (Sahlins 1976). By the mid-1970s, anthropology was becoming increasingly hostile, not to primates, per se, but to the primatologists who sought biological explanations, with an underlying genetic basis, to understand them.⁷

THE EXPANSION OF PRIMATOLOGY

Despite its growing rift with anthropology, primatology was stimulated by the theoretical and methodological tools it had imported from biology. Armed with evolutionary theory, systematic methods, and testable predictions derived from new socioecological models, primatology was poised to expand.⁸ This expansion, which took off during the 1980s, occurred along multiple dimensions that increased both the taxonomic breadth and temporal depth of primate field studies.

The predictive ecological models of behavior being developed at the time were derived from comparisons among a small subset of familiar Old World monkeys and apes that had so far been studied (Southwick and Smith 1986). Whether or not their predictions were applicable to other primates required more extensive field studies on a broader taxonomic diversity of unfamiliar species and a broader ecological array of familiar species. During the 1980s, field primatology attracted U.S. graduate students from anthropology and biology departments alike. This new generation of primatologists was deployed across the world's tropics wherever primates could be found. Neither the phylogenetic nor ecological relevance to human behavioral evolution figured prominently in which species or populations of primates were selected for study because, by this time, the goal of testing predictions from the new comparative models of primate behavioral ecology had taken precedence over studying primates for their insights into hominids.

Field studies designed to evaluate hypotheses in behavioral ecology were also ideally suited to the one to two years that graduate students, and the funding agencies that supported them, could afford to dedicate to their fieldwork. Systematic data on the availability and distribution of food and other ecological resources could be collected concurrently with behavioral data over the course of a 12–24 month study period, and then analyzed to test hypotheses about the effects of ecology on behavior.

A great deal of effort and energy was devoted to characterizing nearly every aspect of primate foods, from their nutritional and energetic contents to their spatial distribution and seasonal availability. Predictions from optimal foraging models (Schoener 1971) about how animals should balance their nutritional and energetic requirements led to analyses of primate feeding, ranging, and grouping patterns, which were seen as compromises among different optima (Emlen 1968; Pyke et al. 1977). Comparative analyses ranged from those of single groups, whose ecologies and behaviors fluctuated across seasons, to those among the same species in different habitats, to those among different species. Intraspecific comparisons could focus on how behavioral variation mapped onto local ecological conditions, while interspecific comparisons, which received more attention, could examine both ecological and phylogenetic influences on behavior.

The accumulation of comparative data led to refinements in the socioecological models. For example, the ecological conditions under which females might cooperate with one another to defend food resources from conspecifics, or avoid one another to reduce competition, led to different sets of predictions about the relative costs and benefits of cooperation and competition within and between groups. Analyses of social relationships and the ways in which kinship and social histories mediated social interactions could be used to evaluate the trade-offs between cooperation and competition. For example, the occurrence of matrilineal societies across a subset of Old World monkeys appeared to coincide with ecological conditions that favored cooperation among kin, and thus was consistent with kin selection's predictions about nepotism (van Schaik 1983, 1989; Wrangham 1980). When food resources could not be cooperatively defended, or invoked intense competition instead, females appeared to avoid one another and, most especially, their closest female kin. Whether these primates lived in patrilocal societies or in groups without any close kin varied with the degree to which cooperation among males was advantageous in competition against other groups of male kin (van Hooff and van Schaik 1992).

The resources over which males cooperated or competed were fertile females instead of food, so both the grouping patterns of females and the timing of reproduction emerged as influences on the social and reproductive options of males (van Hooff and van Schaik 1994). Unlike kinship relationships among females, which could be monitored with observations of maternity and extended matrilineal kin, inferences about paternity and patrilineal kinship were still limited, for the most part, to observations of mating behavior and patrilocal residence patterns, respectively. It was not until the development of methods for analyzing genetic paternity that questions about the fitness consequences of male behavior or nepotism among patrilineal kin could be assessed (Strier in press a).

Ecological and Phylogenetic Approaches Revisited

The taxonomic diversity of primates studied during the 1980s expansion influenced primatology's relationship to anthropology in at least two important respects. For the first time, enough data had accumulated on several species of New World monkeys and prosimians, which include lemurs, lorises, and tarsiers, to reconsider the respective influence of ecology and phylogeny on behavior. For example, the fluid, fission-fusion, male-bonded societies of Central and South American spider monkeys were remarkably similar to those of chimpanzees and consistent with their mutual preferences for ripe fruits typically found in relatively small, indefensible, dispersed patches (Chapman et al. 1995; Symington 1990).

The strong ecological parallels between spider monkeys and chimpanzees were clearly much better predictors of their similar grouping patterns than their distant phylo-

genetic ancestries would imply. At the same time, however, ecology was not sufficient to explain why spider monkeys and their closest relatives, woolly monkeys and muriquis, on the one hand, and chimpanzees and their closest relatives, bonobos, on the other hand, all live in patrilocal societies.

Populations of woolly monkeys and muriquis that include substantial proportions of insects or leaves in their diets, respectively, live in much more cohesive social groups than populations that maintain more frugivorous diets like those of spider monkeys (Di Fiore and Rodman 2001; Moraes et al. 1998; Stevenson et al. 1994; Strier 1992). Similarly, bonobos rely on terrestrial herbaceous vegetation and, correspondingly, live in more cohesive groups than chimpanzees (Chapman et al. 1994). Thus, while ecological variables related to food could account for the differences observed in their grouping patterns, the phylogenetic relatedness among these three genera of New World atelins (muriquis, spider monkeys, and woolly monkeys), on the one hand, and among the two species of *Pan*, on the other hand, appeared to be a better predictor of their similar patrilocal kinship systems (Strier 1994b, 1999a; Wrangham 1987).⁹

Advances in the development of phylogenetic approaches to behavioral adaptations lagged behind those in ecology. Nonetheless, the increased taxonomic breadth spanned by primate field studies made it possible to compare the behavior of primates across phylogenetic groups in increasingly systematic ways (Di Fiore and Rendall 1994). Phylogenetically controlled comparisons have now become a standard in primatology and provide important clues for distinguishing between components of sociality, such as grouping patterns, which can be predicted from local ecological conditions, and those such as kinship patterns and life histories, which appear to be more phylogenetically conservative (Strier 1999a, 2002b).

Phylogenetically controlled comparisons of behavior (or any other trait) seek to identify adaptations as independent evolutionary events (Nunn and Barton 2001). For example, if nothing was known about the shared ancestry of chimpanzees and bonobos, we might conclude that patrilocal evolution evolved independently in each species. Yet, because we know that chimpanzees and bonobos are sister species, it is more likely that both live in patrilocal societies because their last common ancestor did so as well. If patrilocal evolution also characterized early hominids, then it would be treated as a single independent evolutionary event in the taxonomic clade whose living members include humans and both species of *Pan*.

In assessing independent evolutionary events, one begins from the tips of phylogenetic trees and works backward toward each successive node until a behavioral difference that cannot be attributed to shared ancestry is identified. An accurate phylogeny is clearly necessary to this method, and advances in molecular genetics have been critical in refining our understanding of primate

phylogenetic relationships, particularly among closely related species.

To control for phylogeny in behavioral comparisons, one also needs to be able to categorize the behavior of interest, and to know how the behavior is distributed among extant species. The difficulties of classifying continuous behavioral variables, such as the number of males in a group or the degree of sexual dimorphism in male and female body weights, are well-known (Clutton-Brock and Harvey 1984; Moore 1984). However, questions about the information that is lost by reducing intraspecific variation into single, species-specific values have only recently been raised (Strier 1997, 2001b; Struhsaker 2000).

Intraspecific Variation and the Role of Demography

In contemporary phylogenetic approaches, the species (or subspecies, when known) is the smallest unit of comparison. Behavioral data from multiple studies of the same species are compressed into single, species-specific mean or median values, which are then evaluated relative to other species, genera, and so on in each successively inclusive clade. Implicit in this practice is the assumption that interspecific variation will tend to exceed intraspecific variation, and, therefore, the latter can be more or less ignored.

There are several dangers to dismissing intraspecific variation out of hand, but perhaps the most compelling one is that doing so fails to take into account the dynamic processes that shape social behavior in the first place. While the socioecological models of the 1970s and 1980s focused on behavioral responses to deterministic ecological variables, those of the 1990s included the ways in which more facile social variables, often resulting from fluctuations in demography, affected behavior patterns as well.

Long-term data from a variety of studies on a wide range of species now span multiple generations in the primates' lives. Just as comparisons among populations of the same species have demonstrated that primate behavior fluctuates under different ecological conditions (Hill 1999; Yamagiwa and Hill 1998), comparisons across years from single study groups or populations have demonstrated that primates also alter their behavior under different social conditions. Primate social environments are dynamic, and they can undergo dramatic changes during an individual primate's lifetime, as well as from one generation to the next (Strier in press b).¹⁰

The importance of demography for understanding primate social options was recognized decades ago (e.g., Altmann and Altmann 1979; Dunbar 1979; Rowell 1979), but efforts to model how demography, life histories, and behavior interact have only recently received comparative attention. While socioecological studies, which could be completed by dissertators, led to rapid advancements in our understanding of the ways in which ecological variables affect social behavior, comparative insights into so-

ciodemography, which require long-term field data from multiple populations, were much slower to develop.

The lag in incorporating life histories and their demographic consequences into models of primate social behavior is understandable. Primates mature more slowly and live longer than other mammals of their size, so it takes a correspondingly longer time to document the extent of fluctuations in demographic conditions and the social consequences of these fluctuations over an individual's lifespan (Charnov and Berrigan 1993). Relatively long interbirth intervals and correspondingly slow reproductive rates also mean that group and population demographics change over years instead of seasons, necessitating generation-length studies to document.

By the 1990s, however, sufficient long-term field data from a wide range of species made it possible, for the first time, to consider the effects of life histories and demography on behavior from a comparative perspective. It is now clear that groups, as well as individuals, have life histories, and that both group and individual life histories simultaneously influence, and are influenced by, population demography (Strier 1999b). The size and composition of groups are dynamic entities, not static structures, which affect the social options of group members over time. For example, long-term behavioral and genetic data on yellow baboons have shown that a significant proportion of the infants born during the four-year reign of a particularly skillful alpha male were paternally related, in contrast to cohorts born during prior and subsequent years, when social instability and frequent turnovers in the male hierarchy prevented a single male from monopolizing a disproportionate share of fertilizations (Altmann et al. 1996). Although the direction of these fluctuations could not have been anticipated, the opportunities for interactions among paternal kin clearly differ among different cohorts in predictable ways.

Fluctuations in population densities, and stochastic or strategic swings in sex ratios, also impact individual dispersal and reproductive opportunities in predictable ways. Primate responses to these fluctuations can lead to large changes in the size and composition of single groups, with implications for the ways in which behavior patterns are compared. During the past 20 years, the muriqui group I have been studying has tripled in size, with corresponding increases in its members' social options (Strier 2001b). Like the previous examples, it is difficult to interpret the biological significance of the mean or median group size during this 20-year period, yet these values have been calculated and used in comparative phylogenetic analyses of behavior by other researchers. Whether or not such compression of temporal fluctuations or trends into a single population or species value affects the outcome of the analyses is an empirical question that has not yet, to my knowledge, been systematically explored.

The dynamics of primate demography also affect the viability of populations. Growing interest in conserving the world's endangered primates and advances in conservation

biology have converged with the accumulation of demographic and life history data to emphasize the importance of populations instead of particular groups or species, and the effects of both ecological and demographic stochasticity instead of determinism.

In conservation biology, populations and their characteristics are the defining elements that determine a species' probability of extinction (Strier 1997). Unlike study groups, populations contain the genetic variation on which selection pressures can act, and, therefore, the size, composition, and geographic distribution of populations affect their long-term viabilities and, ultimately, those of the species to which they belong (Lacy 1993). The importance of populations in analyses of extinction risks has compelled many primate conservationists to split species into smaller units, or taxa, in order to recognize the intraspecific variation that populations contain (Mittermeier et al. 2000; Rylands et al. 1997).¹¹

Population Variation and the Future Place of Primatology

The shift in primatology to its present, more population-oriented perspective is a positive step toward reuniting it with anthropology. It is ironic, perhaps, that primatology's more recent links with conservation biology would contribute to the new populationist thinking in primatology and offset, to some extent, the emphasis that phylogenetic models put on interspecific comparisons or that evolutionary biology put on ecological determinism. After all, population biology employs the quantitative methods of other biological disciplines, while both phylogenetic and ecological interests in primates were, at least initially, almost entirely ethnographically oriented.

It is even more curious that primatologists working within reductionist biological paradigms would be quicker to identify population variation than primatologists trained as anthropologists, whose sensitivity to the vast behavioral diversity of humans should have made us more alert to the possibility and significance of intraspecific variation in other primates as well. Anthropocentric preconceptions about the distinctiveness of humans versus other primates seem to have extended to include a double standard for evaluating the extent and significance of intraspecific diversity.

Cultural Primatology

The renewed interest in primatology among cultural anthropologists and archaeologists may be attributed, at least in part, to the recent comparative analyses of local "traditions" in chimpanzee populations that cannot be explained by ecological or phylogenetic differences among them (de Waal 1999; McGrew 1998, 2001; McGrew et al. 2001; Whiten et al. 1999). Chimpanzees are not the only primates to exhibit population variation in tool use or social customs, but their behavioral plasticity appears to be greater, at least so far, than it is in other nonhuman pri-

mates (Huffman 1984; Huffman and Quiatt 1986; McGrew 1998, 2001; van Schaik et al. 1999). Ecological conditions that permit social tolerance, a prerequisite for the social transmission of behavior, and advanced cognitive abilities, must clearly be involved in the flexible adoption of local behavior patterns for which no genetic basis can be ascribed (van Schaik et al. 1999; van Schaik and Knott 2001). Ideas about the effects of local ecological conditions on variation in levels of social tolerance converge with ideas about the influence of local demographic conditions on varying social options across populations as well (Mitani and Watts 1999; Strier 2000). Whether such cases of population variation in behavior are best understood as local "cultural" traditions may still be controversial because primatologists and other anthropologists still disagree about definitions of culture. Nonetheless, it is clear that refining prior assumptions about species-typical behavior to include the role of learning on local behavioral traditions represents a compelling area of mutual interest among primatologists and other anthropologists (McGrew 2001).

Deciphering how local traditions, whether for food acquisition or reinforcing social relationships, are transmitted within populations has a long history in primatology. Yet the new examples of local traditions that have emerged in recent years have renewed efforts to understand the underlying mechanisms involved. The development of appropriate methodologies to systematically document and compare interpopulation variation in the behavior of primates has just begun (McGrew 2001), stimulating primatologists to take into account some of the same kinds of factors that cultural anthropologists have long considered. Together with refinements in ecological, phylogenetic, and demographic models of social behavior, understanding the processes involved in the social transmission of behaviors may provide clues into understanding the potential of different primates, including human populations, to adapt.

Reconciling Approaches to Intraspecific Diversity

The socially mediated transmission of local behavioral traditions is not the only area in which contemporary primatology and other areas of anthropology intersect. For example, some of the classic analyses of human societies, such as those of Robin Fox (1975) involving the interactions among patterns of kinship, mating (or marriage), and alliances, can serve as templates for evaluating the social constraints and genetic consequences of the diversity of dispersal and mating patterns among primates (Moore and Ali 1984; Strier 2002b). The distribution of kinship systems and their correlates among primates, like those among humans, reflect historical (evolutionary), ecological, and social influences and have obvious social, as well as biological (and genetic), consequences. Conversely, advances in the ways in which primates, including humans, negotiate within their social networks to establish and

maintain valued relationships (e.g., Aureli and de Waal 2000; Noë et al. 2001) represent a convergence of interest by primatologists in questions of long-standing interest to other anthropologists.

Contemporary primatology is still coping with the challenge of sorting out the relative influence of ecology, phylogeny, and, more recently, demography on both intra- and interspecific behavioral variation. In primatology, efforts to distinguish predictable and unpredictable patterns of intraspecific variation have lagged behind those to distinguish patterns of interspecific variation. In anthropology, by contrast, characterizing and interpreting the behavioral diversity of humans is, by definition, an exercise in understanding intraspecific variation. Merging the phylogenetically controlled, systematic methods of primatology with the cross-cultural comparative approaches of anthropology (e.g., Mace and Holden 1999) is just one example of the many ways in which primatology and other areas of anthropology can continue to converge.

Understanding the relative importance of intra- and interspecific variation in primates is also a critical step toward understanding the differences and similarities that exist between humans and any other species of primates. It should therefore be of central interest to both biological and nonbiological anthropologists. Whether the range of intraspecific behavioral variation expressed by humans falls within or beyond that expressed by any other species of primates depends, in part, on the behaviors being compared. Comparisons among humans, like those among other species of primates, are more persuasive when based on data that have been collected in comparable, standardized ways.

Anthropology's Responsibility to Primatology

The convergence of interest in advancing our understanding of intraspecific variation among both human and nonhuman primates extends beyond intellectual questions to the much more urgent concerns of conservation. Habitat loss and disturbances now threaten nearly one-third of the world's primates with extinction (Mittermeier et al. 1999; Mittermeier et al. 2000). Despite global conservation efforts, the pace at which primate populations and their habitats are being decimated exceeds the pace at which biological adaptations, which require the duration of entire generations, can occur. The ability of primates to adjust their behavior more rapidly on shorter time frames, in response to the new ecological and demographic challenges they face, will determine which populations, and ultimately which species, will survive.

Considering that anthropogenic activities account for the most serious threats to the world's primates today, it is highly appropriate that anthropologists take a greater interest in primatology than they have in the recent past. Archaeological studies of the impact of prehistoric humans on their environments provide perspectives on the impact of contemporary humans. Similarly, areas of cul-

tural anthropology, such as cultural ecology, medical anthropology, and economic anthropology, can provide perspectives on the factors that affect human patterns of resource use and abuse. Insights from these and other specializations in anthropology bear directly on the future of other primates, and on the steps that may be necessary to protect them.

Understanding the tremendous behavioral variation and adaptive potential of all primates is an urgent challenge for which primatologists and anthropologists must unite. Now, once again, the place of primatology lies within anthropology, but, ironically, this time it is because of the perspectives on other primates that humans can provide.

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NOTES

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1. Populations, which are traditionally defined as the individuals of a species that share genes, provide the contexts in which behavior—and evolution—occur. Comparative data from multiple populations of a species are necessary to identify the species-specific traits that are relevant for comparisons with the human species.

2. This review focuses primarily on the relationship between primatology and other areas of U.S. anthropology. Perspectives on the culture of primatology in other countries can be found in other recent reviews (e.g., Strum and Fedigan 2000).

3. Sussman (2000) provides a fascinating history of how interest in nonhuman primates as models for early hominid behavioral evolution emerged in response to the changing views of hominids, many of which were presented at the Cold Spring Harbor Symposium of Quantitative Biology held in June 1950 and published in 1951.

4. Many other primatologists were using systematic methods of behavioral sampling prior to this time, but standardized methods became widely established with Altmann's (1974) influential article.

5. Like any scientific discipline, advances in primatology have been, and continue to be, dependent on collecting the appropriate data needed to evaluate, and reject, prevailing hypotheses.

6. Evolutionary models of behavior have been criticized on a variety of grounds, including, but not limited to, their apparent failure to consider the possibility of alternative explanations. For example, without knowledge of genetic relatedness, it is difficult to distinguish the preferential treatment of familiar associates, which may also happen to be kin, from nepotism as postulated by kin selection. Similarly, the common use of terms such as *strategies* to describe behavior implies a level of intentionality on the part of actors that have little, if any, awareness about the fitness consequences of their actions.

7. It is curious that the ecological and evolutionarily deterministic approaches adopted by primatologists, and the relativist approaches adopted by cultural postmodernists, represented such divergent solutions to the same problems of accounting for observer biases and understanding behavioral variation. Although primatologists are in no way unique among anthropologists in their use of quantitative methods, the more fluent they became in the language of biology, the less intelligible they were to many nonbiological anthropologists.

8. It is important to emphasize that tests of any prediction, no matter how carefully stated or theoretically well founded, are only as powerful as the data on which they are based.
9. The influence of ecology on primate grouping patterns has been supported by both inter- and intraspecific comparisons across a wide range of species. For example, mountain gorillas and Venezuelan red howler monkeys are strikingly similar to one another in their behavioral ecologies despite their phylogenetic distance as hominoids and ceboids, respectively (Sterck et al. 1997).
10. The great potential many primates display to adjust their behavior in response to local or fluctuating variables in their social environments raises a fundamental question about the degree to which behavior is molded by past evolutionary selection pressures, which may not have been constant or unidirectional.
11. Conservationists acknowledge that some of the new taxonomic designations are based on sparse data but provide a persuasive rationale that it is better to err on the side of preserving biodiversity than risk its loss through extinction.

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